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TRICHECODON HUXLEYI (MAMMALIA: ODOBENIDAE)
IN THE PLEISTOCENE OF SOUTHEASTERN
UNITED STATES

BY CLAYTON E. RAY

WITH TWO PLATES

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NO. 3 — *TRICHECODON HUXLEYI* (*Mammalia: Odobenidae*) in the
Pleistocene of southeastern United States

BY CLAYTON E. RAY

In 1877 Joseph Leidy (pp. 214-216, Pl. 30, fig. 6) described and illustrated the tusk of a fossil mammal from the Ashley River phosphate beds, near Charleston, South Carolina. He referred the specimen, with reservations, to the modern Atlantic walrus. This tentative Pleistocene record for the modern walrus, together with its climatic implications, has been accepted uncritically by biogeographers and paleoecologists to the present day (cf. Deevey, 1949, p. 1375; Dorf, 1959, pp. 184, 196). Recently, my own attempts to identify a fossil tusk (University of Florida No. 3274) found near Sarasota, Florida, have led me to re-examine the South Carolinian and other occurrences of fossil walruses. Aside from the living walrus, here treated as a single species (cf. Scheffer, 1958, p. 84; Davies, 1958, p. 102), and Quaternary specimens clearly pertaining to it,¹ the only form with which the Sarasota specimen can be compared usefully is *Trichecodon huxleyi* Lankester 1865,² from the Pleistocene of Europe. The tusks of other extinct forms are either unknown (*Prorosmarus*) or poorly known (*Alachtherium*; Hasse, 1910, p. 303).

DESCRIPTION

Judging from its slight curvature in the frontal plane, which, although variable, is characteristically mesad in walruses, the Sarasota specimen is apparently from the right side and will be so considered for purposes of description. The dimensions of the specimen are given in Table 1. The natural surface of the tusk is composed of a thin, smooth layer of cementum, still preserved

¹ These include, with the exception of the record for the Ashley River, those records cited by Kellogg (1922, pp. 49-51, *Trichecodon* was then considered to be Pliocene) and by Hay (1923, pp. 21-29), together with more recent reports by Allen (1930), Borissiak (1930), Dow (1954), Handley (1953), Matsumoto (1926), Norton (1930), and Palmer (1944).

² Lankester (1880, pp. 213-216) has shown beyond doubt that the name *Trichecodon* rests with his East Anglian fossils and not with the Belgian material of van Beneden (1877). Whether *Trichecodon* is congeneric with *Odobenus* must be determined on the basis of the European material, and is thus outside the scope of this paper.

Table 1. Measurements of tusk of *Trichecodon hurleyi*
from Florida, U.F. 3274.

	mm.
Length along outer curve	435.0
Length in straight line	406.0
Greatest anteroposterior diameter	93.0
Greatest transverse diameter	56.9
Ratio of greatest transverse diameter to greatest anteroposterior diameter	.61
Greatest circumference	240.0
Least anteroposterior diameter	55.3
Least transverse diameter	34.3
Least circumference	90.8
Maximum thickness of cementum preserved	2.6
Long diameter of pulp cavity at proximal end	68.0
Short diameter of pulp cavity at proximal end	28.9
Long diameter of osteodentinal tube at distal end (estimated)	25.5
Short diameter of osteodentinal tube at distal end (estimated)	9.3
Depth of open pulp cavity (minimum)	60.0

for the most part. The dominant surface features are two strongly developed longitudinal grooves on the flattened medial surface (Plate 1A), both of which diminish in depth distally to the point of disappearance at the extreme tip of the tusk, perhaps due in part to wear. A similar, but weaker, groove is present on the posteromedial surface of the tusk. On the lateral, convex side are several lesser longitudinal grooves, largely smoothed out on the surface, but clearly shown where the cementum is missing (Plate 2). The cementum is thick in the grooves and thin on the intervening ridges, the effect of which is to mask the grooves. This condition is probably due to differential wear rather than to an initial variation in thickness of cementum deposited. The ridges are exposed to, and the grooves protected from, wear. The cementum is sharply differentiated by weathering into a firm, black, inner layer of variable thickness (owing to the fluting) and a flaky, gray, outer layer averaging 1-1.5 mm. in thickness. A small area of the extremely smooth outer surface of the unweathered layer is exposed by the exfoliation of weathered cementum at the distal extremity of the tusk (Plate 1B). At least some of the subsurface flutings persist to the distal extremity of the tusk as revealed in section at the broken distal

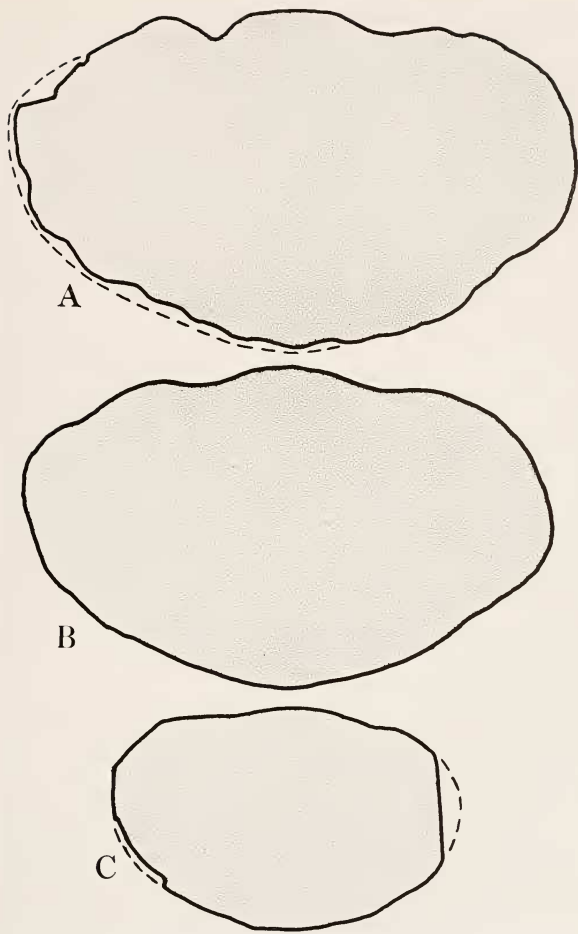


Figure 1. Transverse sections A, B, and C of U.F. 3274 at the points A, B, and C respectively, indicated on Plate 1B. The medial surface is upper, and anterior is to the right in each section. $\times 1$.

end. The fluted dentinal surface is marked by transverse striations or growth lines, which appear in Plate 2 as alternating light and dark bands (owing to the presence of light colored clay in the valleys between ridges), averaging about 9-10 of each per centimeter. The shape of the transverse section of the tooth is roughly that of a flattened ovoid with the medial side plano-convex and deeply grooved and the lateral side smoothly convex (Fig. 1). The tusk is rather strongly curved in the parasagittal plane. Its inner curvature forms an arc of a circle with a radius of about 45 centimeters, and its outer, of about 40 centimeters. These figures represent only the crudest of approximations, since the curvature is not constant throughout the length of the tusk. The degree of external curvature is strongly increased in the distal 10 centimeters of the tusk, as a result of natural wear which produced a flattened facet on the outer curvature (Fig. 1C). The tusk is also curved very gently mesad. The base of the open pulp cavity is occupied by a projecting mass of globular osteodentine (Plate 2), which fills the cavity solidly distad from the base, as revealed at the fractured distal end of the tooth. The tooth tapers abruptly distad, a feature enhanced by the wear on the outer curvature. Except for the distal 10 centimeters of the tooth, the curvature and taper shown represent very nearly the initial, unworn condition. If either feature were due largely to wear, the osteodentine would be exposed on the outer curvature of the tooth (cf. Lankester, 1880, p. 219, figs. 1, 2, and Mansfield, 1958, p. 26, fig. 5). The small amount of wear, deep, open pulp cavity, and unrestricted proximal end indicate that the tooth belonged to a sub-adult or adult (but not senile) individual.

The general form and structure together with the characteristic globular osteodentine leave no doubt that the tooth belongs to a walrus-like mammal. The presence of osteodentine, the ovoid cross-section, and the absence of "engine-turning" in the dentine rule out the possibility of its belonging to a proboscidean. However, certain discrepancies prevent the assignment of the tusk to *Odobenus rosmarus*. Although it is not certain that the true outer surface is anywhere preserved in the fossil, the sheath of cementum is apparently thinner than that of *O. rosmarus*. The maximum thickness of cementum measurable on the fossil is 2.6

mm.; that of a sectioned tusk of *Odobenus rosmarus* (M.C.Z. 21638), 4.0 mm. The maximum anteroposterior diameter of the fossil tusk is 10 millimeters greater than that of any modern walrus in the Museum of Comparative Zoology (19 adult individuals). Its maximum circumference equals that of the world's record Atlantic walrus and is exceeded only by the first and second-place Pacific walruses (Webb, et al., 1952, pp. 155, 158). These latter two individuals may be taken as approaching the absolute maximum in robustness for *Odobenus rosmarus*, since they represent maxima obtained from the world's major collections. It is improbable that the fossil lies at the upper size limit of its species. The deep, persistent, longitudinal surface grooves on the medial face and the fluting of the dentinal surface on the lateral face cannot be matched in *O. rosmarus*. The transverse striations are not interspersed with widely separated, strong, transverse (annual?) ridges, as they are in *O. rosmarus* (cf. Brooks, 1954, p. 40, fig. 7, and Mansfield, 1958, p. 31, fig. 7, p. 35, fig. 8A). The fossil is more flattened transversely than is typical of *O. rosmarus*. The curvature of the tusk exceeds that typically seen in *O. rosmarus* (cf. Rutten, 1907, Table 1). Its curvature can be matched very nearly by the right tusk of M.C.Z. 7301 (which owes its great curvature in part to extreme wear on the outer curvature), but otherwise exceeds that of any tusk in the Museum of Comparative Zoology. The initial taper of the fossil tusk is much greater than that of any Recent tusk examined.

It is of great interest to note that Leidy (1877, pp. 215-216) observed almost exactly the same dissimilarities between the tusk from the Ashley River phosphate beds and those of the modern walrus, all of which led him to suspect that his fossil represented a distinct species, which wisely he did not describe on the basis of his single example of such a variable element. Comparison between the Sarasota fossil and Leidy's description and figure ³ reveals striking similarities in gross size, curvature, taper, and fluting. The maximum anteroposterior and transverse diameters are almost identical. Leidy's specimen has a reduced transverse diameter at its proximal extremity, indicating old age and

³ The specimen was part of a temporary exhibition of fossils belonging to the Pacific Guano Company. Recent correspondence has failed to reveal its presence in the Academy of Natural Sciences of Philadelphia or in the Charleston Museum.

cessation of growth, as is seen in old specimens of *O. rosmarus* and in *Trichecodon hurleyi* (Rutten, 1907, p. 4).

Leidy evidently did not compare his specimen with *Trichecodon hurleyi* and his paper is not cited by the subsequent writers on *Trichecodon* (van Deinse, 1943-44, Hasse, 1910, Rutten, 1907, and Lankester, 1880). Kellogg was aware of all the literature, but his paper was a review and did not deal with any of the material at first hand. These lapses may be explained in part by *Trichecodon*'s having been assigned to the Tertiary, until recently, and to the very general lack of transatlantic liaison. The characters of the tusks from Sarasota and Charleston are exactly those diagnostic of *Trichecodon hurleyi*. These include robust form, great curvature, abrupt tapering, lateral compression, prominent surface and subsurface fluting, uniform transverse striation on dentinal surface, and thin cementum (Lankester, 1865, 1880; Rutten, 1907). In the aggregate, these features readily distinguish *T. hurleyi* from *O. rosmarus*, but no one character can be regarded as absolute. For example, the degree of lateral compression can be expressed in terms of the ratio of transverse to anteroposterior diameters. A series of 30 Recent tusks of *O. rosmarus* in the Museum of Comparative Zoology gives a mean ratio of .68 and a range of .59-.82. Comparable figures for eight tusks of *T. hurleyi* are .59 and .48-.71.⁴ Six of the eight tusks of *T. hurleyi* have ratios of .59 or less. The Floridian and South Carolinian tusks have ratios of .61 and .59 respectively. Thus, on the basis of lateral compression alone, the American fossils fit more comfortably into *T. hurleyi* but cannot be excluded absolutely from *O. rosmarus*. That there is great variation and thus considerable overlap between species in these non-occluding teeth is not at all surprising. On the basis of all characters mentioned above, the specimens from southeastern United States may be assigned confidently to the extinct form.

PROVENANCE

The Floridian tusk was found in August, 1957, "near the edge of a marl pit in a new housing development, De Soto Lakes.

⁴ The standard statistical operations were not carried out, since neither species is represented by an adequate sample. Most of the skulls of *O. rosmarus* are unsexed and without locality.

where they were digging shell for their roads. . . . De Soto Lakes is about six miles from the present shore of Sarasota Bay, and about the same distance northeast of the center of the city of Sarasota, virtually on the line between Sarasota and Manatee Counties" (Murray, *in litt.*, April 27, 1959). According to the records and well logs of the Florida Geological Survey the Miocene Hawthorn Formation is overlain by no less than 20 feet of Pleistocene deposits in the vicinity of De Soto Lakes (Olsen, *in litt.*, June 1, 1959). Exploratory cores drilled 12 miles east northeast and 21 miles due east of De Soto Lakes reveal Pleistocene terrace sands 44 and 35 feet thick respectively (Catheart and McGreevy, 1959, pls. 23, 24, 34). The marl is probably Pleistocene in age and represents the reworked top of the Hawthorn Formation. A sample of sand extracted from the pulp cavity of the tusk and examined by Dr. Jules R. DuBar, is considered by him to be more like the Miocene than like the Pleistocene sands of the area.

Few if any of the vertebrate fossils from the Ashley River phosphate beds bear precise locality or stratigraphic data owing to their incidental recovery in the course of commercial operations. Most of the fossil mammals are clearly of Pleistocene age, but some of the marine mammals are of probable Miocene aspect (Allen, 1926, p. 447).

The English specimens of *T. huxleyi* come primarily from a triangular area in Suffolk delimited by lines joining the towns of Ipswich, Oxford, and Walton-on-the-Naze. Most of the fossils are derived from the so-called Nodule Bed or Suffolk Bone Bed, a discontinuous, thin deposit, possibly in part reworked from older strata, at the very base of the Red Crag Series (Chatwin, 1954, pp. 42-57; Lankester, 1880, pp. 213, 216; Newton, 1891, p. 17). The Red Crag Series, formerly thought to include strata as old as Miocene, is now assigned to the earliest Pleistocene (Charlesworth, 1957, pp. 599, 1016; Chatwin, 1954, p. 42). *T. huxleyi* has also been recorded from the Cromer Forest Bed on the basis of a single tusk (Newton, 1882, p. 26; a second fragmentary tusk showed resemblances to that of *O. rosmarus*), and doubtfully from the Chillesford Beds at Aldeby on the basis of the proximal half of a femur (Newton, 1891, p. 17). The Cromer Forest Bed, which overlies the Red Crag Series, is

generally assigned to the first interglacial (Charlesworth, 1957, p. 1016; Zeuner, 1959, pp. 137-138).

The fine skull referred by Rutten to *T. huxleyi* was dredged from the sea near Breskens, West Scheldt, Zeeland, Netherlands. Rutten, influenced by the supposed Pliocene age of the Red Crag Series, attributed a Pliocene age to the Dutch fossil. The overgrowth of barnacles, perfect preservation, and considerable organic content suggest a Quaternary age for the specimen. Van Deinse (1943-1944, pp. 97-101) has subsequently reported upon two almost perfect skulls found in the same vicinity. Hooijer (1957, p. 256) has assigned these and all the "black bones" of the Scheldt estuary to the base of the Pleistocene and correlated them with the Nodule Bed of the Red Crag Series. Thus, according to current stratigraphic interpretations, *T. huxleyi* is known definitely only in the Pleistocene.⁵ I am unable to determine the affinities of the fragmentary tusk from the vicinity of Antwerp inadequately described by van Beneden (1877, p. 47 and Pl. VI, fig. 8) and considered by Lankester to pertain to *T. huxleyi*.

PALEOECOLOGICAL SIGNIFICANCE

It is perhaps significant that *Trichecodon* is unknown from the cold-water members of the Crag Series, but occurs in the basal bed of the Red Crag Series, probably in the Chillesford Beds, and in the Cromer Forest Bed, all of which were laid down under temperate conditions (Zeuner, 1959, p. 143). The occurrence of *T. huxleyi* in the southeastern United States suggests that it was an inhabitant of warmer waters than is the living walrus. One hesitates to invoke boreal conditions in the surface waters of the Gulf of Mexico, as would appear to be necessary for *Odobenus rosmarus*. If such conditions prevailed, the terrestrial Pleistocene fauna of peninsular Florida, the climate of which is profoundly influenced by adjacent seas, would certainly have reflected such cooling, and it does not. It seems probable that the southerly limits of the range of *T. huxleyi* extended into warm-temperate seas.

⁵ Although I consider it to be unlikely, it must be admitted that the nature of the stratigraphy at the De Soto Lakes, Charleston, and East Anglian localities together with the nature of the fossils discovered at these localities (isolated tusks and a fragmentary femur only) leaves open the possibility that the fossils could be reworked from deposits as old as the Miocene. The fine Dutch material could scarcely have been redeposited.

The amphi-Atlantic distribution of *T. hurleyi* is not unexpected and is analogous to the distribution of *Halichoerus grypus* (cf. Davies, 1958, p. 110). Like the grey seal, it may never have spread into the Pacific Ocean, owing to an aversion to subarctic waters (assuming also that its range never extended far enough south to utilize the Central American water route).

With the elimination of the South Carolinian record for *Odobenus rosmarus*, the most southerly extension of the range of this species in the Pleistocene recedes northward some 230 miles to Kitty Hawk, North Carolina at 36° 03' north (Hay, 1923, p. 29).⁶ In Europe the most southerly Pleistocene localities for *O. rosmarus* are in the vicinity of Paris (Montrouge, 48° 50' north, and Saint-Menehould, 49° 04' north; Kellogg, 1922, p. 50). Before commenting upon these records it is necessary to discuss the Recent distribution of the walrus. Unfortunately, the walrus is firmly and erroneously associated with Arctic conditions in popular thinking and in much of the scientific literature. Allen (1930) has called attention to the fact that the walrus bred on Sable Island off Nova Scotia (44° N.) at least through 1650 and was recorded off Cape Breton as early as 1583. The number of specimens dredged from New England waters (Allen, 1930; Dow, 1954; Palmer, 1944) and a live record for Plymouth in 1734 (Allen, 1930) suggest the possibility of regular seasonal occurrence south perhaps to Cape Cod within Recent time. In Europe the walrus apparently frequented (and bred upon?) the Orkney Islands (59° N.) through 1550 (Ritchie, 1921, p. 8) and is still reported occasionally in North Sea waters (Ritchie, 1921, pp. 8, 9, 77 et seq.; Mohr, 1952, pp. 251-254). Very little importance can be attached to the sporadic southerly occurrences of the walrus, since occasional widely extra-limital records are the rule among marine mammals. However, Sable Island and northernmost Scotland clearly did lie within the normal range of the walrus in historic time. Both Sable and Orkney Islands lie near the southern limits of the boreal sea (Clench and Turner,

⁶ There is in the University of Florida collections (U.F. 2112) a small fragment of the worn distal end of a walrus tusk from St. Mary's, Camden County, Georgia. Its thin cementum, fluting, lateral compression, and transverse striations are suggestive of *Trichecodon*, but I regard the specimen as generically indeterminable. Dorf (1959, p. 196) states that "walrus bones have been found . . . as far as South Carolina and Georgia," which is correct only in the sense that Charleston is as far south as, indeed farther south than, much of (inland) Georgia. I am aware of no published record for the walrus in Georgia.

Ms. Zoogeographic provinces of the western Atlantic; Feyling-Hanssen, 1955, p. 25).⁷ Thus, on a uniformitarian basis, a minimum hypothesis to account for the Pleistocene distribution of *O. rosmarus* would shift the southern limit of the boreal sea south to Kitty Hawk on the west and to Paris on the east. Kitty Hawk lies nearly 600 miles south of Sable Island, and Paris nearly 700 miles south of Orkney. In Recent time the range of the walrus extended 15° farther south in the western Atlantic than in the eastern. The fossil evidence indicates a figure of 13° for the Pleistocene, suggesting that similar zoogeographic zones extended farther south in the western than in the eastern Atlantic during the Pleistocene, just as they do today.

It seems likely that *T. huxleyi* ranged to the south of *O. rosmarus* on either side of the Atlantic. During glacial epochs both forms would have moved southward, with *T. huxleyi* becoming separated into American and European populations in southeastern United States (Florida and South Carolina records) and (hypothetically) southwestern Europe, while *O. rosmarus* extended its range southward to Kitty Hawk and Paris, though presumably maintaining its transatlantic connection in the north. During preglacial and interglacial epochs both forms would have moved northward, with *T. huxleyi* re-establishing transatlantic interchange between the previously isolated populations in northeastern North America (hypothetical) and northern Europe (English and Dutch records), while *O. rosmarus* retreated into high latitudes, undoubtedly establishing connection with the Pacific population at times (Davies, 1958, pp. 102-103).

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⁷ It might be argued that Arctic seas extended farther south at the time when walrus occurred in these southerly localities, but they were already exterminated or nearly so by the onset of the "Little Ice Age" about 1650 (Dorf, 1959, p. 199).

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